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COMMUNITY STRUCTURE OF HERMATYPIC CORALS AT LAYSAN ISLAND AND LISIANSKI ISLAND/NEVA SHOAL IN THE NORTHWESTERN HAWAIIAN ISLANDS: A NEW LAYER OF SCIENTIFIC EXPLORATION

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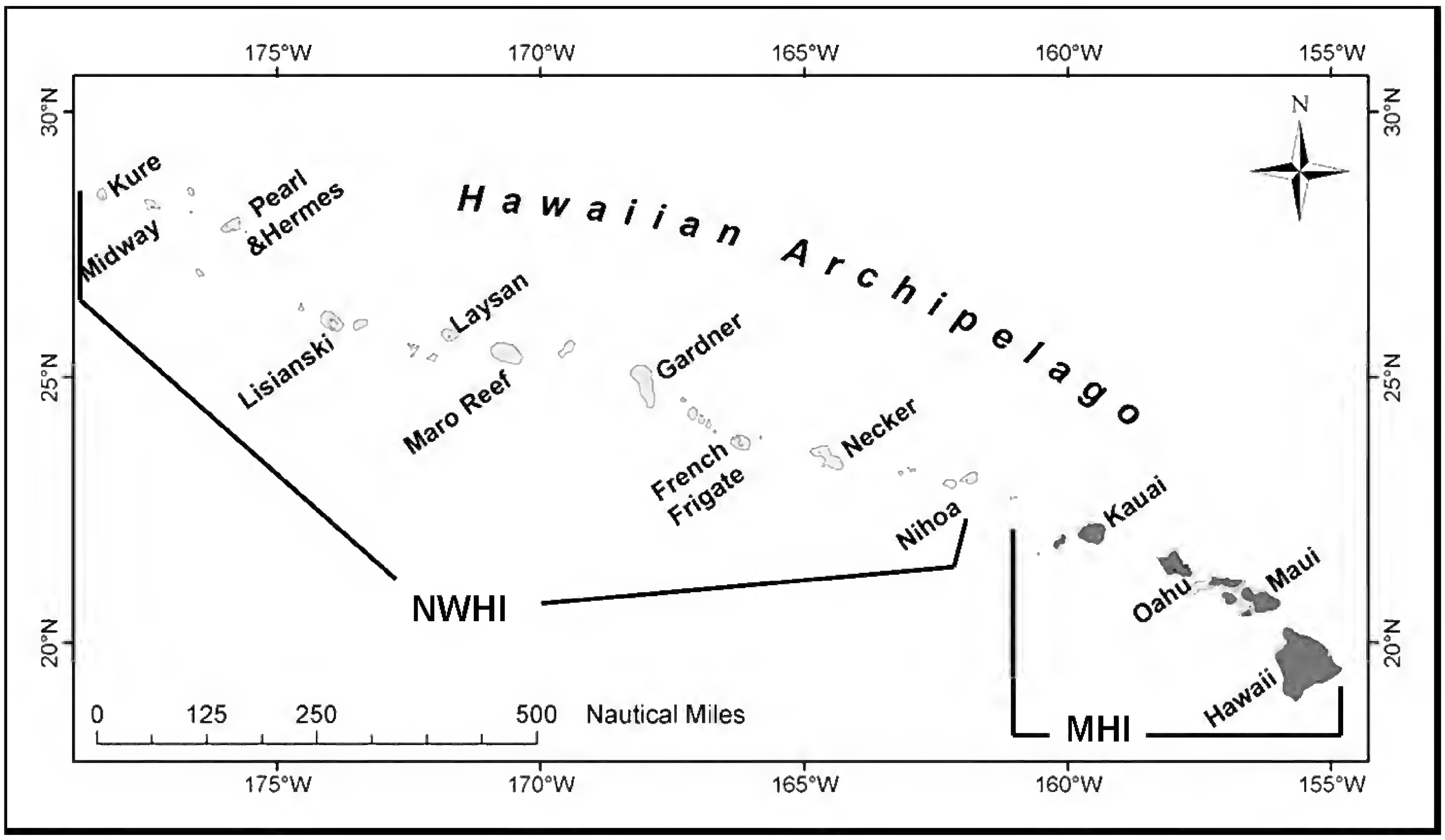

Figure 1. The Hawaiian Archipelago. NWHI = Northwestern Hawaiian Islands; MHI = main Hawaiian Islands. Lightly shaded areas represent 100-fathom isobaths.

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ABSTRACT

The distribution and abundance of scleractinian corals at Laysan Island and Lisianski Island/Neva Shoal in the Northwestern Hawaiian Islands were determined by georeferenced towed-diver surveys that covered more than 56,000 m2 of benthic habitat and site-specific surveys at 33 sites during 2000 - 2004. Three complementary methods (towed-diver surveys, videotransects, and photoquadrats) were used to quantify percent cover of corals by genus or species at each bank and determine relative abundance. Colony counts within belt transects at fixed sites were used to assess colony density and size-class distribution. Significant differences were found between the two banks at comparable depths (7-18 m) in percent coral cover, relative abundance of the three primary genera (*Porites*, *Montipora*, and *Pocillopora*), and size class distributions of these genera. The coral community at Lisianski/Neva Shoal was characterized by higher percent cover, higher colony density, and a tendency towards larger colonies than the coral community at Laysan. *Porites* was the dominant genus at both locations, but the relative abundance of *Pocillopora* and *Montipora* differed between the banks, with *Pocillopora* more common at Laysan than at Lisianski/Neva Shoal, and *Montipora* more common at Lisiansksi/Neva Shoal than at Laysan. Notable differences were also found in the distribution of the three primary genera at the two banks. These demographic data are discussed in the context of the known history of exposure of these remote reefs to salient factors influencing the condition of coral communities including marine debris, bleaching, and disease. They provide a detailed baseline of the composition of these shallow-water communities in the early years of the 21st century that will serve as a comparative benchmark for examining long-term change.

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INTRODUCTION

One of the first steps in science is often simple description. The history of scientific exploration in the Hawaiian Archipelago spans more than 160 years, in the course of which paradigm-shifting discoveries such as the theory of evolution and plate tectonics have been proposed, debated, accepted, and widely woven into the fabric of scientific thought. Leading scientific discoveries such as these depend on the insightful interpretation of an accumulation of more mundane, detailed data. As the number of unexplored terrestrial places becomes fewer, scientific explorers increasingly turn to the oceans and to space as the relatively unknown frontier which, as a first step, must necessarily be described.

Laysan Island (25°46′N, 171°45′W) and Lisianski Island (26°04′N, 173°58′W) are carbonate islands in the Northwestern Hawaiian Islands (NWHI) (Fig. 1) that were formed about 17 and 20 million years ago, respectively, as an underlying shield volcano and a portion of the associated coral reef bank were lifted above sea level (NOAA, 2003). Seafaring Polynesians may have been aware of the presence of these islands (Athens et al., 2007) well before the discovery of Lisianski by a Russian exploring vessel in 1805 (Clapp and Wirtz, 1975) or the discovery of Laysan by an American whaling ship in the 1820s (Ely and Clapp, 1973). The native biota of both islands was ravaged in the late 19th and early 20th century by feather collecting for the millinery trade and by the introduction of herbivorous rabbits; Laysan was additionally disrupted by extensive guano mining from 1891 to 1903 (Ely and Clapp, 1973; Clapp and Wirtz, 1975). In response to pressure from conservation groups, in 1909 Theodore Roosevelt established the Executive Order proclaiming all of the islands from Kure to Nihoa, with the exception of Midway, as the Hawaiian Islands Bird Reservation, a preserve for native birds. Other forms of political protection and management authority since that time, including the creation of the NWHI Coral Reef Ecosystem Reserve through Executive Orders in 2000 and 2001 by William J. Clinton, culminated in the designation through Presidential Proclamation by George W. Bush of Papahānaumokuākea Marine National Monument in June 2006, in recognition of the unique ecological attributes of both terrestrial and marine habitats in the NWHI.

Both islands are surrounded by banks capable of supporting shallow (10 fathom, ~ 18 m) and deeper (10-100 fathom, ~ 183 m) coral reef ecosystems. The shallow-water (~ 18 m) bank area surrounding Laysan Island measures 26.4 km^2 while the extensive bank (Neva Shoal) that surrounds Lisianski Island is more than eight times as large (215.6 km^2, Rohmann et al., 2005). Prevailing northeast trade winds generate wave regimes that chiefly impact northeast and eastern exposures during the summer; mean wave power increases in the winter, particularly on north and northwest sectors exposed to the storm-generated North Pacific swell (Friedlander et al., 2005). Early scientific studies in the NWHI, such as the Tanager Expedition of 1923-24, focused almost exclusively on avifauna and terrestrial vegetation (Ely and Clapp, 1973; Clapp and Wirtz, 1975). With the advent of SCUBA in the mid 20th century and the implementation of the Cooperative Quadripartite Program conceived by four state and federal agencies (Grigg, 2006), quantitative in situ studies of coral communities were first conducted throughout

the NWHI in the early 1980s (Grigg, 1983). The creation of the NWHI Coral Reef Ecosystem Reserve in 2000 generated a new wave of scientific exploration and discovery in this region, enhanced by modern technologies including GPS (global positioning system), GIS (geographic information system), digital imagery, and remote sensing. The growth of knowledge made possible by enhanced technologies and increased survey effort is exemplified by the number of coral taxa reported in the scientific literature within the last century. An early 20th century study (Vaughn 1907) described 21 nominal species of corals collected at Laysan. Grigg (1983) reported 18 coral species from Laysan and 17 from Lisianski/Neva Shoal. The most recent published studies report 29 species of scleractinian corals from Laysan and 26 from Lisianski/Neva Shoal (Maragos et al. 2004). At least two additional species, in the genus *Acropora*, were discovered at Lisianski/Neva Shoal in 2006 (Maragos, pers. comm.)

Historical observations of terrestrial biota, such as those provided by Schauinsland (1899) at Laysan in 1896 just prior to the massive impacts to the island from guano mining, commercial feather collection, and devegetation by rabbits, have proved to be invaluable benchmarks by which to compare modern conditions (e.g., Athens et al., 2006). Marine ecosystems, including those in remote, politically protected regions like the NWHI, may be poised on a trajectory of change driven by factors such as global warming and its attendant consequences of sea level rise and ocean acidification (Kleypas et al., 2006). This paper describes the community structure of the shallow-water (< 20 m) scleractinian corals at Laysan and Lisianski/Neva Shoal, based on surveys conducted in 2000-2004 using three complementary methods. These data are then placed in the context of other physical and biological factors known to influence the nature and condition of coral communities, including wave stress, marine debris, bleaching, and disease. Unique in its detail and spatial scale, this study serves as an important baseline describing these coral communities in the early years of the 21st century, one that will serve as a reference point for future marine scientists and managers.

MATERIALS AND METHODS

Benthic surveys

Towed-diver surveys were primarily conducted in 2000 (21-29 September) and 2002 (15-30 September) according to the methods of Kenyon et al. (2006c). Several additional surveys were conducted at each location in 2003 (23-26 July) and 2004 (24 September-11 October) to examine habitat that had not been assessed on earlier surveys. On 2000 and 2002 surveys, a digital videocamera inside an underwater housing with a wide-angle port was used to continuously record benthic imagery. On 2003-2004 surveys, a digital still camera (Canon EOS-10D, EF 20mm lens) in a customized housing with strobes was used to photograph the benthos automatically at 15-sec intervals. Habitat digital videotapes recorded in 2000 and 2002 were sampled at 30-sec intervals (inter-frame distance ~ 23 m) and quantitatively analyzed for coral percent cover using the methods of Kenyon et al. (2006c). Digital photographs recorded in 2003 and 2004

were sampled at 30-sec intervals and quantitatively analyzed for coral percent cover using point-count software (Coral Point Count with Excel Extension, Kohler and Gill, 2006), using 50 randomly stratified points per frame. The coral categories that could be distinguished were *Pocillopora*, massive and encrusting *Porites* (e.g., *P. lobata*, *P. evermanni*), *P. compressa*, *Montipora*, and other live coral (e.g., *Pavona*, *Fungia*, faviids). Laser-projected dots used to calibrate image size did not appear on videographic imagery recorded during 2002 surveys because of mechanical problems. Average depth was calculated for the photo-documented portion of each towed-diver survey from an SBE 39 temperature/pressure recorder (Sea-Bird Electronics, Inc.) mounted on the habitat towboard, and survey distances were calculated using GPS and ArcView GIS 3.3.

Site-specific belt-transect surveys, along with digital video recording of benthic cover along the transect lines, were independently conducted by three separate teams of divers at Laysan on 15-18 September 2002 and at Lisianski/Neva Shoal on 16 September -2 October 2002 according to the general methods described by Maragos et al. (2004) for 2002 Rapid Ecological Assessments. Nine additional sites were surveyed at Lisianski/Neva Shoal on 9-11 October 2004 using the same methods. Locations of sitespecific surveys were determined on the basis of: (1) filling gaps in the locations of baseline assessments conducted during an expedition to the NWHI in 2000; (2) depths that allowed three dives/day/diver; (3) constraints imposed by other ship-supported operations; and (4) sea conditions. Detailed methods for recording videographic and size class data are presented in Kenyon et al. 2006b.

With the exception of one site at Lisianski/Neva Shoal, 12 (35 cm x 50 cm) photoquadrats were concurrently photographed at each site with spatial reference to the same two 25 m transect lines (i.e., 6 photoquadrats per transect) according to the methods of Preskitt et al. (2004).

Data Extraction and Analysis

Capture, sampling, and analysis of frames from videotransects are described in Kenyon et al. 2006b. The taxa that could be identified were *Pocillopora meandrina*, *P. damicornis*, massive and encrusting *Porites* (e.g., *P. lobata, P. evermanni), Montipora capitata*, *M. patula*, *Pavona duerdeni*, *Fungia*, *Leptastrea*, and *Cyphastrea ocellina*. Detailed methods for determining coral percent cover from photoquadrat imagery are also presented in Kenyon et al. 2006b.

Transect site locations and tracks of towed-diver surveys georeferenced with nondifferentially corrected GPS units (Garmin® model 12) were mapped using ArcView GIS 3.3. For analytical purposes, towed-diver and site-specific surveys were grouped spatially according to one of four geographic sectors (NE, SE, SW, and NW), so as to examine coral cover and taxonomic relative abundance based on exposure to or shelter from the direction of primary wave regimes. Towed-diver surveys that spanned more than one geographic sector were subdivided into separate sectors using the time stamp that linked GPS position to digital imagery. At Lisianski/Neva Shoal, towed-diver surveys conducted in shallow (< 5.4 m average depth) inshore waters were also grouped and analyzed separately from towed-diver surveys conducted in deeper (> 7.4 m average depth) offshore waters.

At each bank, differences in total percent coral cover among sectors were examined using Kruskal-Wallis tests, as data sets were not normally distributed even with transformations. Differences in the percent cover of coral genera among sectors at each bank were examined using the chi-square test of independence among two or more samples; at Laysan, taxa were aggregated as *Porites*, *Pocillopora*, and *Montipora*, while at Lisianski/Neva Shoal taxa were aggregated as *Porites, P. compressa,* and *Montipora*. A Mann-Whitney rank sum test was used to examine differences in total coral cover between the two banks; the chi-square test was used to compare differences in relative abundance of coral taxa between the banks. The size frequency distributions of *Porites*, *Montipora*, and *Pocillopora* were each compared between banks with the KolmogorovSmirnov two-sample test. Statistical analyses were conducted using SigmaStat® software.

Maragos et al. (2004) provide two indices of the relative occurrence and abundance of 29 coral species at Laysan and 26 species at Lisianski/Neva Shoal based on qualitative Rapid Ecological Assessment surveys at 22 and 37 sites, respectively. Methods described in Kenyon et al. 2006b were used to compare these indices with the relative abundance of coral species as determined by percent cover analysis of photoquadrats in this study.

RESULTS

Laysan

Towed-diver surveys

The distance between sample frames analyzed at 30-sec intervals from benthic tow imagery depends on the tow speed; the average inter-frame distance ranged from 19.4 m to 30.5 m (mean = 23.4 m, n = 13 tows). The average benthic area captured in laser-scaled frames was 2691 cm^2 (SE = 88 cm^{2,} n = 331 frames). Towed divers surveyed 25.2 km of benthic habitat (Table 1, Fig. 2), from which 1107 frames were analyzed. Given the 3:4 aspect ratio of the frames and extrapolating to the total number of consecutive, non-overlapping still frames that compose the benthic imagery, this benthic analysis area (1107 frames x 0.2691 m^2/frame = 298 m^2) samples a total survey area of 15,095 m^2 (Table 1).

Total average coral cover across the bank was low, ranging from 3.6% in the southeast sector to 7.3% in the northwest, with a bank-wide average of 5.3% (Table 1, Fig. 3a). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, H = 68.31, df = 3, p < 0.001). The differences among the four sectors in the relative abundance of coral genera present were also statistically significant (chi-square test, X^2 = 27.8, df = 6, p < 0.001). Massive and encrusting *Porites* (e.g., *P. lobata, P. evermanni*) dominated across the bank, accounting for close to 70% or more of the coral cover along all exposures. The contribution of *Pocillopora* to total coral cover was highest along eastern exposures. *Porites compressa* contributed a small amount (< 10%) to coral cover on all sectors. *Montipora* contributed little to coral cover across the bank (Table 1, Fig. 3a).

Site-specific surveys: video transects

A total of 288 m^2 at 9 sites (32 m^2/site) were quantitatively assessed from transect videotapes. Average coral cover ranged from 2.9% in the northeast sector to 15.3% in the northwest sector, with a bank-wide average of 8.2%, (Table 2, Fig. 3b). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 36.95$, df = 3, $p < 0.001$).

Only five scleractinian taxa were seen in Laysan video transects (*Porites lobata*, *P. evermanni*, *Pocillopora meandrina*, *Montipora patula*, and *Pavona duerdeni*). The differences among the four sectors in the relative abundance of coral genera present were statistically significant (chi-square test, $X^2 = 188.4$, df = 6, $p < 0.001$). Massive and encrusting *Porites* (*P. lobata, P. evermanni*) dominated across the bank with the exception of the northeast exposure, where *Pocillopora meandrina* dominated. *Porites compressa* was not seen in any videotransects. *Montipora* contributed a small amount (< 10%) to coral cover on all sectors.

Site-specific surveys: photoquadrats

Videotransects and photoquadrats were recorded concurrently at 9 sites. The maximum difference in total coral cover calculated with the two methods was 3.4%; the average of the absolute values of the difference between video transect and photoquadrat total coral cover for all 9 sites was 1.5%. The overall patterns of coral composition and cover were highly similar to those derived from videotransects (Table 2, Figs. 3b, 3c). Average coral cover ranged from 2.3% in the northeast sector to 13.7% in the northwest sector, with a bank-wide average of 7.6%, (Table 2, Fig. 3c). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 26.63$, df = 3, $p < 0.001$).

Only five scleractinian taxa were seen in Laysan photoquadrats (*Porites lobata*, *P. evermanni*, *Pocillopora meandrina*, *Montipora patula*, and *Cyphastrea ocellina*). The differences among the four sectors in the relative abundance of coral genera present were statistically significant (chi-square test, $X^2 = 214.9$, df = 6, $p < 0.001$). Massive and encrusting *Porites* (*P. lobata, P. evermanni*) dominated across the bank with the exception of the northeast exposure, where *Pocillopora meandrina* dominated. *Porites compressa* was not seen in any photoquadrats. *Montipora* contributed a moderate amount (< 20%) to coral cover on southern exposures.

Site-specific belt-transect surveys: colony density and size classes

A total of 1255 colonies were counted and classified by their maximum diameter within belt transects covering 600 m^2 at 11 sites. *Porites* was the most numerically abundant (i.e., highest density) taxon across the bank followed by *Pocillopora*, *Montipora*, faviids, and *Pavona* (Fig. 4). The average colony density for all taxa combined was 2.1 colonies/m^2.

Table 1. Coral cover determined from towed-diver surveys conducted at Laysan and Lisianski/Neva Shoal, NWHI, 2000–2004.

Bank	Geographic sector	Distance surveyed (km)	Area surveyed[a] (m^2)	Range of average depth (m)	Average % total coral cover	Proportion of total coral cover[b]: Massive & encrusting *Porites*	*Porites compressa*	*Pocillopora*	*Montipora*	Other live coral
Laysan	ALL	25.2	18566	9.6–17.8	5.3	79.9	5.1	13.1	1.5	0.4
	NE	7.0	5157		4.7	68.4	2.9	24.1	2.4	2.2
	SE	6.5	4789		3.6	76.3	8.1	15.6	0.0	0.0
	SW	6.6	4863		6.0	92.3	1.3	4.3	2.0	0.0
	NW	5.1	3757		7.3	80.9	8.0	9.7	1.0	0.4
Lisianski deeper offshore	ALL	43.2	33887	7.4–14.3	19.7	52.3	25.2	1.1	21.2	0.3
	NE	13.8	10825		13.9	49.3	16.7	1.0	32.9	0.1
	SE	11.3	8864		24.9	47.6	32.7	0.8	18.7	0.2
	SW	10.7	8393		27.3	42.2	37.7	1.1	18.8	0.2
	NW	7.4	5805		9.9	82.9	8.7	1.6	5.8	0.9
Lisianski shallow inshore	ALL	9.4	6925	1.4–5.4	11.8	5.5	5.0	1.4	88.2	0.1

[a] Area surveyed is based on average area of laser-calibrated frames captured at 30-sec intervals.
[b] Proportions are graphically presented in Figures 3a and 7a.

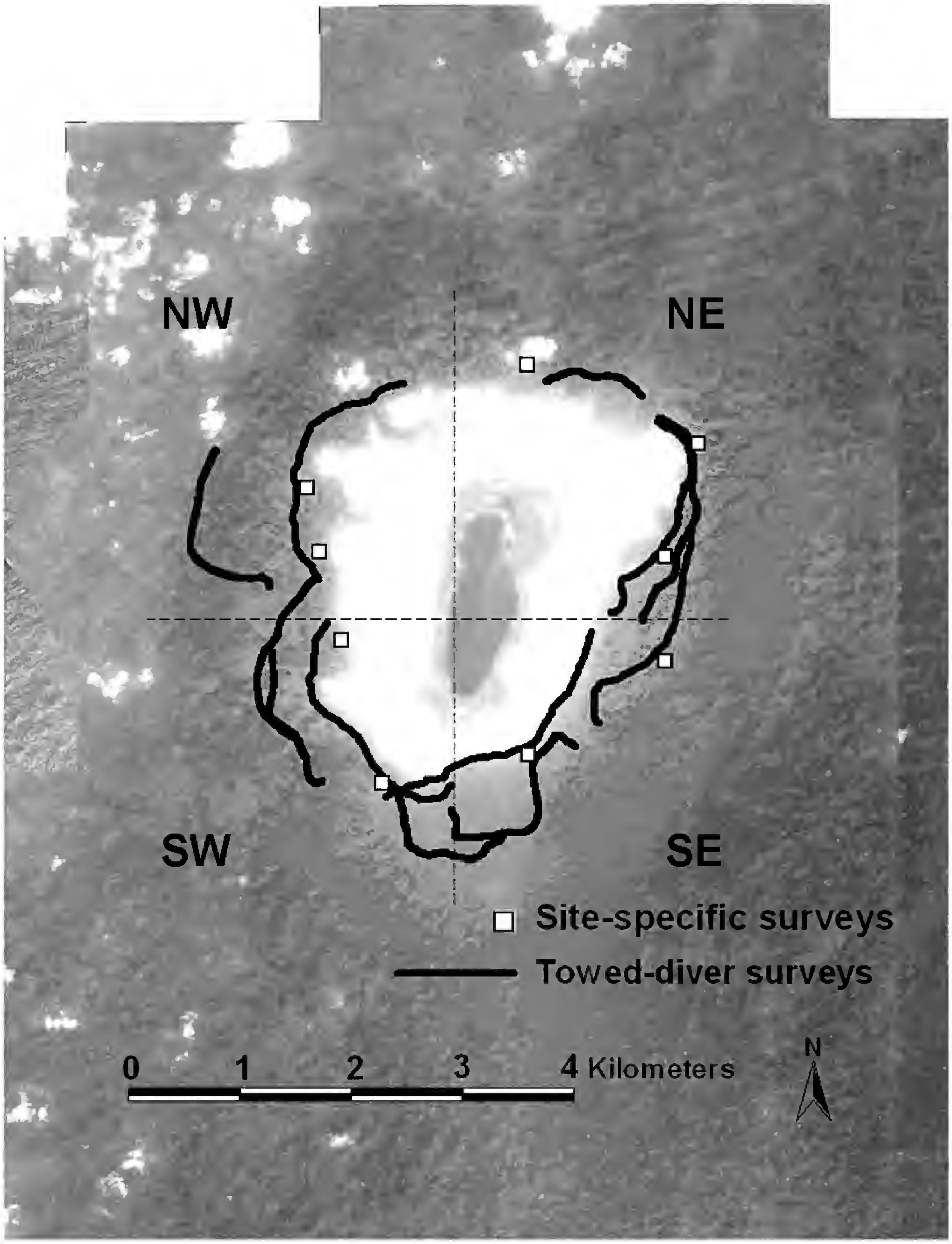

Figure 2. Location of towed-diver and site-specific surveys at Laysan, NWHI, using IKONOS satellite imagery as a base map.

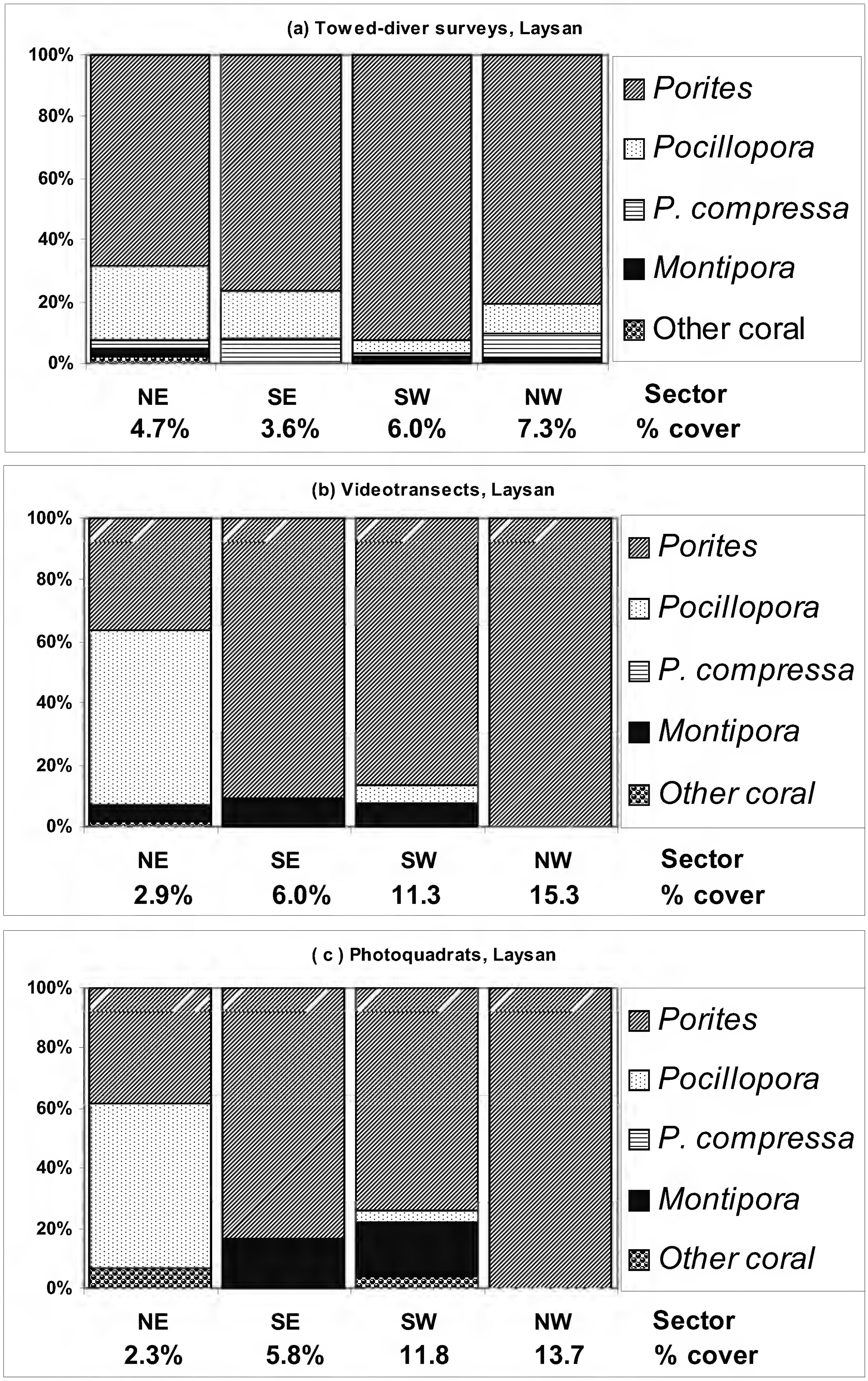

Figure 3a – c. Relative abundance of primary coral taxa by geographic sector at Laysan, NWHI, derived from three different methods. Values below labels are total coral percent cover within each sector. *Porites* = massive and encrusting *Porites*.

Table 2. Coral cover determined from video transects and photoquadrats conducted at Laysan, NWHI, in 2002.

				Proportion of total coral cover[b]				
Exposure	# Sites surveyed	Average total percent coral cover[a]	Range of transect depths (m)	massive & encrusting *Porites*	*Porites compressa*	*Pocillopora*	*Montipora*	Other coral
VIDEO TRANSECTS								
ALL	9	8.2	10.0–12.1	70.3	0.0	23.6	5.5	0.6
NE	3	2.9		36.1	0.0	56.9	5.2	1.8
SE	2	6.0		90.7	0.0	0.0	9.3	0.0
SW	2	11.3		86.8	0.0	5.7	7.5	0.0
NW	3	15.3		99.8	0.0	0.0	0.2	0.0
PHOTOQUADRATS								
ALL	9	7.6	10.0–12.1	70.0	0.0	19.2	7.8	3.0
NE	3	2.3		38.4	0.0	54.9	0.0	6.7
SE	2	5.8		83.3	0.0	0.0	16.7	0.0
SW	2	11.8		73.9	0.0	3.9	18.4	3.8
NW	2	13.7		100.0	0.0	0.0	0.0	0.0

[a]Values are means of replicate transects (2/site) or photoquadrats (12/site).

[b]Proportions are graphically presented by sector in Figures 3b and 3c.

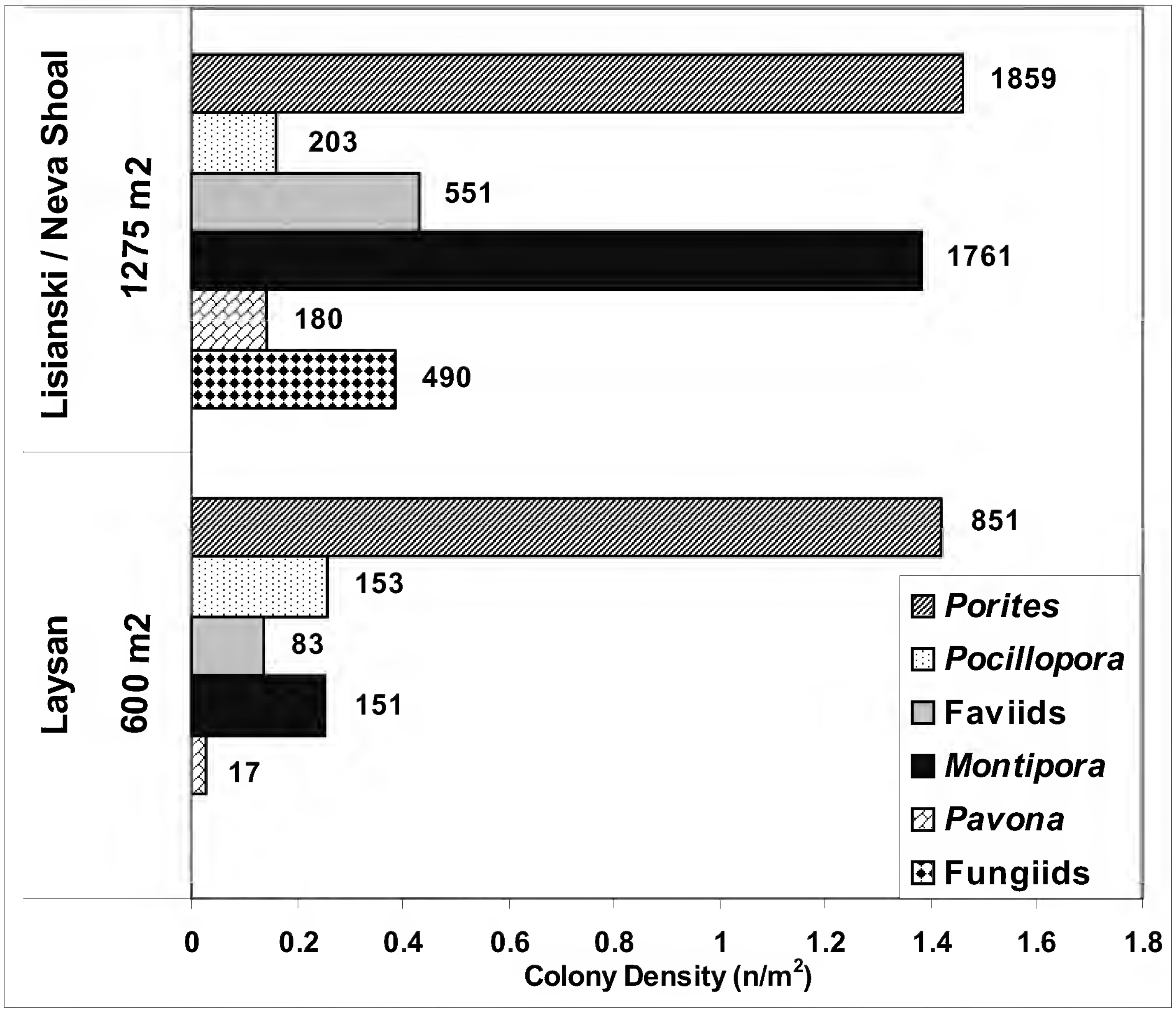

Figure 4. Colony density (n/m^2) of six coral taxa at Laysan and Lisianski/Neva Shoal, NWHI. Number of colonies (n) was determined from belt transect surveys; area (m^2) surveyed at each bank is shown next to bank label. Values to the right of bars are the number of colonies of each taxon.

Each of the three primary coral genera at Laysan (*Porites, Montipora*, *Pocillopora*) had distinctive size class distributions (Fig. 5). *Porites* colonies achieved the largest sizes in addition to making the highest contribution to percent cover (Fig. 3) and having the highest density (Fig. 4). *Montipora* colonies, while contributing little to percent cover (Fig. 3), also showed a broad range of size classes, with fairly even representation in all but the largest (> 80 cm) size classes. Large colonies (> 40 cm) constituted 18% of all *Porites* colonies enumerated, and 15% of all *Montipora* colonies enumerated. *Pocillopora*, most abundant on the northeast sector (Fig. 3), showed a bellshaped distribution centered in the 10-20 cm size class.

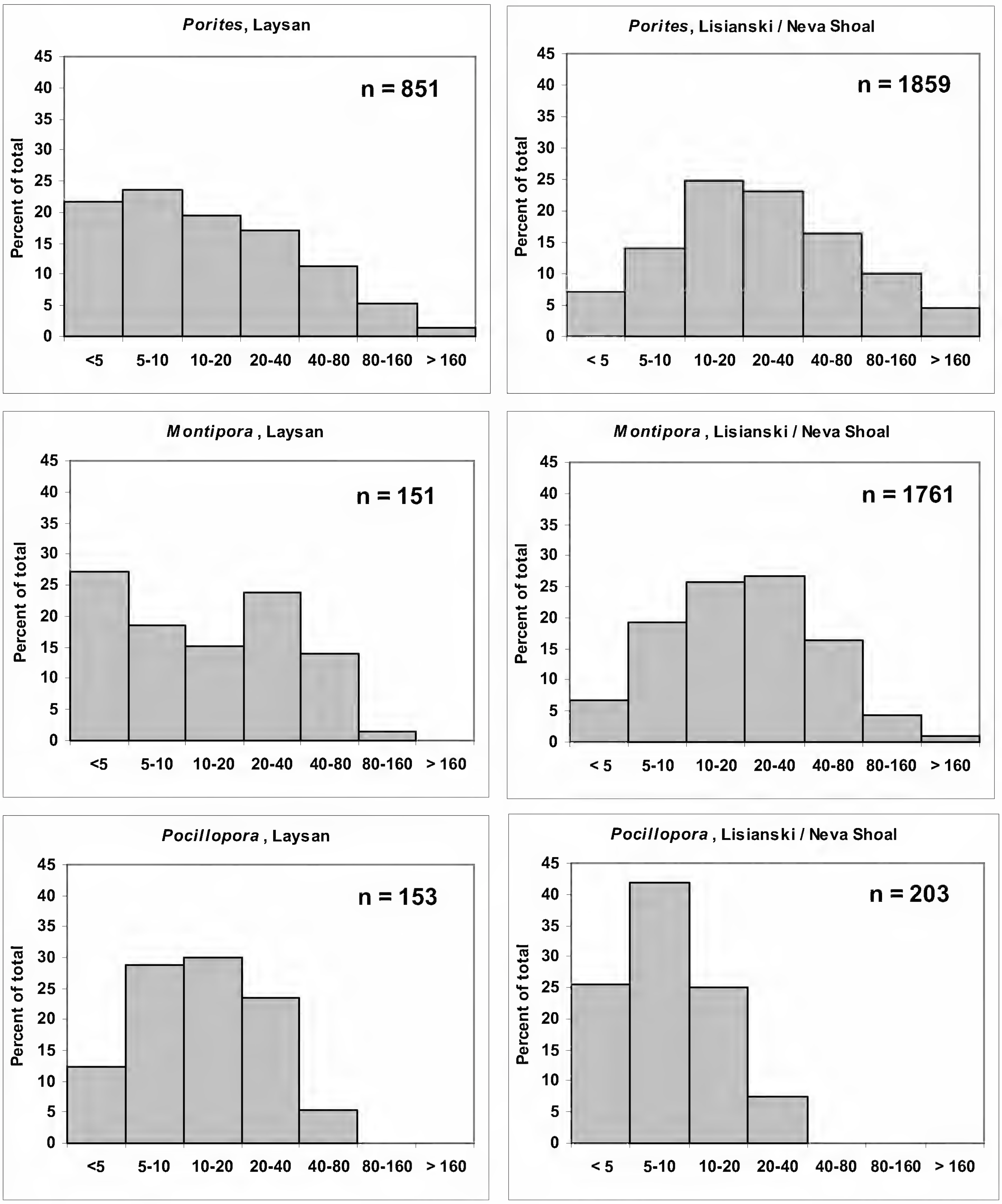

Figure 5. Size class (cm) distributions of primary scleractinian corals at Laysan and Lisianski/Neva Shoal, NWHI.

Lisianski/Neva Shoal

Towed-diver surveys

The average inter-frame distance ranged from 18.7 m to 28.0 m (mean = 23.0 m, n = 19 tows), and the average benthic area captured in laser-scaled frames was 4615 cm^2 (SE = 119 cm^2, n = 840 frames). Towed divers surveyed 43.2 km of deep (> 7.4 m) offshore benthic habitat and 9.4 km of shallower (< 5.4 m) inshore benthic habitat (Table 1, Fig. 6), from which 1873 frames were analyzed. This benthic analysis area (1873 frames x 0.4615 m^2/frame = 864 m^2) samples a total survey area of 41,261 m^2 (Table 1).

From surveys assessing deep (> 7.4 m) offshore habitat, total average coral cover across the bank was low to moderate, ranging from 9.9% in the northwest sector to 27.3% in the southwest, with a bank-wide average of 19.7% (Table 1, Fig. 7a). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 126.44$, df = 3, $p < 0.001$). The differences among the four sectors in the relative abundance of coral genera present were also statistically significant (chi-square test, $X^2 = 60.6$, df = 6, $p = < 0.001$). Massive and encrusting *Porites* (e.g., *P. lobata, P. evermanni*) dominated across the bank, accounting for more than 40% of the coral cover along all exposures. *Montipora* or *P. compressa* codominated along all exposures except the northwest. *Pocillopora* contributed little to coral cover across the bank (Table 1, Fig. 7a).

Surveys assessing shallow (< 5.4 m) inshore benthic habitat (Fig. 6) indicated total average coral cover was moderately low (11.8%). *Montipora* dominated the shallow inshore coral community, accounting for 88.2% of the total coral cover (Table 1).

Site-specific surveys: video transects

A total of 480 m^2 at 15 sites (32 m^2/site) were quantitatively assessed from transect videotapes. Average coral cover ranged from 14.7% in the northwest sector to 38.5% in the northeast sector, with a bank-wide average of 25.4% (Table 3, Fig. 7b). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 111.62$, df = 3, $p < 0.001$).

Ten scleractinian taxa were seen in Lisianski/Neva Shoal video transects (*Porites lobata*, *P. evermanni*, *P. compressa*, *Pocillopora meandrina*, *P. damicornis, Montipora patula, M. capitata*, *Pavona duerdeni, Cyphastrea ocellina, and Fungia*). The differences among the four sectors in the relative abundance of coral genera present were statistically significant (chi-square test, $X^2 = 111.2$, df = 6, $p < 0.001$). Massive and encrusting *Porites* (*P. lobata, P. evermanni*) dominated on western exposures, but *Montipora* dominated along eastern exposures (Table 3, Fig. 7b). *Porites compressa* was most abundant along western exposures. *Pocillopora* contributed little (< 1%) to coral cover on all sectors.

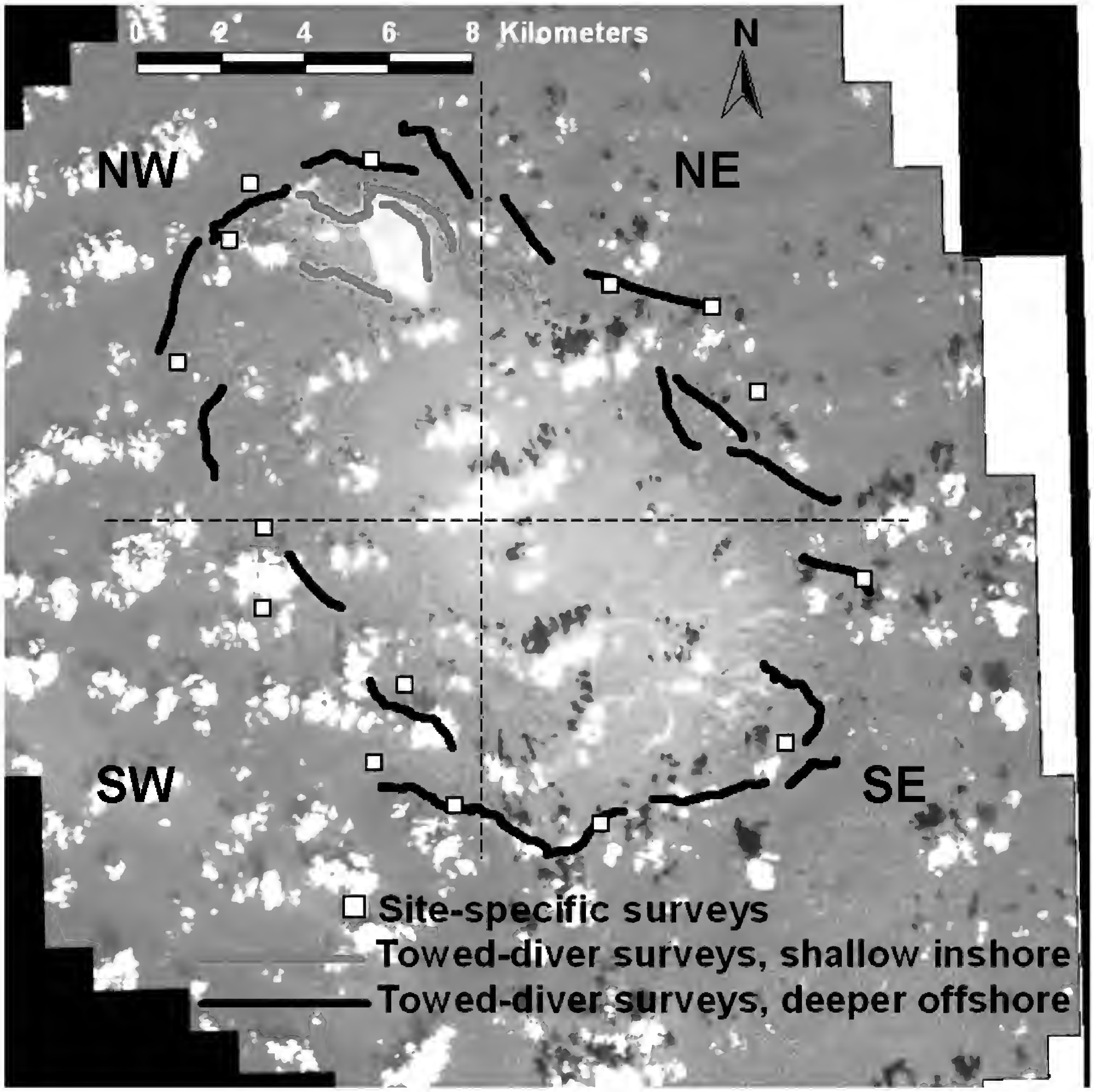

Figure 6. Location of towed-diver and site-specific surveys at Lisianski/Neva Shoal, NWHI, using IKONOS satellite imagery as a base map.

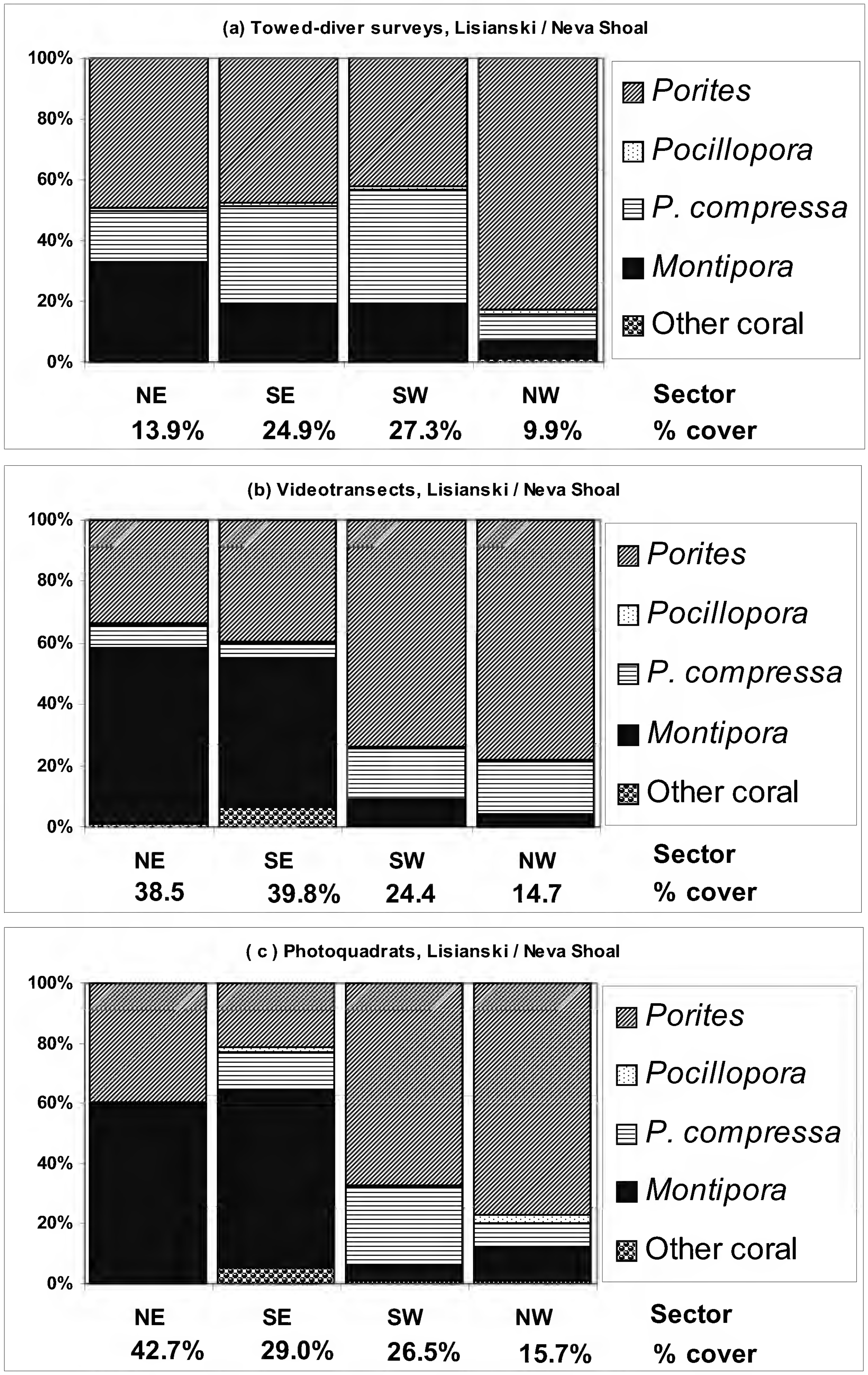

Figure 7a - c. Relative abundance of primary coral taxa by geographic sector at Lisianski/Neva Shoal, NWHI, derived from three different methods. Only deeper (> 7.4 m) towed-diver surveys are shown to simplify the graphic. Values below labels are total coral percent cover within each sector. *Porites* = massive and encrusting *Porites*.

Site-specific surveys: photoquadrats

Videotransects and photoquadrats were recorded concurrently at 14 sites. The maximum difference in total coral cover calculated with the two methods was 6.9%; the average of the absolute values of the difference between video transect and photoquadrat total coral cover for all 14 sites was 3.7%. The overall patterns of coral composition and cover were highly similar to those derived from videotransects (Table 3, Figs. 7b, 7c). Average coral cover ranged from 15.7% in the northwest sector to 42.7% in the northeast sector, with a bank-wide average of 27.2%, (Table 3, Fig. 7c). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 23.54$, df = 3, $p < 0.001$).

Nine scleractinian taxa were seen in Lisianski/Neva Shoal photoquadrats (*Porites lobata*, *P. evermanni*, *P. compressa*, *Pocillopora damicornis, Montipora patula, M. capitata*, *Cyphastrea ocellina, Psammocora stellata, and Fungia*). The differences among the four sectors in the relative abundance of coral genera present were statistically significant (chi-square test, $X^2 = 148.1$, df = 6, $p < 0.001$). Massive and encrusting *Porites* (*P. lobata, P. evermanni*) dominated on western exposures, but *Montipora* dominated along eastern exposures (Table 3, Fig. 7b). *Porites compressa* was most abundant along the southwestern exposure. *Pocillopora* contributed little (≤ 3%) to coral cover on all sectors.

Site-specific belt-transect surveys: colony density and size classes

A total of 5096 colonies were counted and classified by maximum diameter within belt transects covering 1275 m^2 at 22 sites. *Porites* and *Montipora* were the most numerically abundant (i.e., highest density) taxa across the bank followed by faviids, *Fungia*, *Pocillopora*, and *Pavona* (Fig. 4). Only 52 colonies (of *Psammocora stellata*) did not belong to these taxa. The average colony density for all taxa combined was 4.0 colonies/m2.

Porites and *Montipora* had bell-shaped size class distributions at Lisianski/Neva Shoal (Fig. 5). Both taxa achieved the largest sizes in addition to making the highest contribution to percent cover (Fig. 7) and having the highest densities (Fig. 4), with 31% of *Porites* colonies and 22% of *Montipora* colonies belonging to large (> 40 cm) size classes. *Pocillopora*, uncommon in all sectors (Table 3, Fig. 7), was predominantly characterized by small (< 10 cm) colonies.

Laysan vs. Lisianski/Neva Shoal

In deeper habitats (> 7.4 m) surveyed by towed divers, there was a statistically significant difference between Laysan and Lisianski/Neva Shoal in average total percent coral cover (Mann Whitney rank sum test, $T = 1473287$, $p < 0.001$), with higher coral cover at Lisianski/Neva Shoal than at Laysan. Similarly, there was a statistically significant difference between Laysan and Lisianski/Neva Shoal in average total percent coral cover using both videotransect data (Mann Whitney rank sum test, $T = 63167$, $p <$

Table 3. Coral Cover determined from videotransects and photoquadrats at Lisianski/Neva Shoal, NWHI, 2002 and 2004.

				Proportion of total coral cover[b]				
Exposure	# Sites surveyed	Average total percent coral cover[a]	Range of transect depths (m)	Massive & encrusting *Porites*	*Porites compressa*	*Pocillopora*	*Montipora*	Other coral
VIDEO TRANSECTS								
ALL	15	25.4	7.3–14.2	62.3	13.2	0.6	22.8	1.1
NE	3	38.5		33.4	7.5	0.6	57.3	1.1
SE	2	30.4		39.8	4.9	0.2	48.9	6.2
SW	6	24.4		73.8	16.2	0.8	9.0	0.3
NW	4	14.7		78.2	17.0	0.4	4.4	0.0
PHOTOQUADRATS								
ALL	14	27.2	6.7–14.5	57.6	13.7	1.3	26.0	1.4
NE	3	42.7		40.1	0.4	0.5	59.0	0.1
SE	2	29.0		21.4	12.7	1.4	59.1	5.5
SW	5	25.5		67.3	26.6	0.4	4.9	0.9
NW	4	15.7		76.9	8.1	3.0	11.2	0.9

[a]Values are means of replicate transects (2/site) or photoquadrats (12/site).

[b] Proportions are graphically presented by habitat in Figures 7b and 7c.

0.001) and photoquadrat data (Mann Whitney rank sum test, $T = 9600$, $p < 0.001$), with higher coral cover at Lisianski/Neva Shoal.

All three methods showed a statistically significant difference between Laysan and Lisianski/Neva Shoal in the relative proportion of coral taxa, as assessed through percent cover data (chi-square test; towed-diver surveys, $X^2 = 45.2$, df = 3, $p < 0.001$; videotransects, $X^2 = 47.7$, df = 3, $p < 0.001$; photoquadrats, $X^2 = 40.8$, df = 3, $p < 0.001$). *Pocillopora* was uncommon at Lisianski/Neva Shoal (≤ 1.3% of coral cover, all three methods) but accounted for > 13% of cover (all three methods) at Laysan, where it was especially prevalent in the northeast sector. Conversely, *Montipora* was uncommon at Laysan (≤ 7.8% of coral cover, all three methods) but accounted for > 21% of cover (all three methods) at Lisianski/Neva Shoal, where it was especially prevalent along eastern exposures. *Porites compressa* was also more common in deeper habitats at Lisianski/Neva Shoal (> 13%, all three methods) than at Laysan (≤ 5.1%, all three methods).

Overall coral colony density was nearly twice as great at Lisianski/Neva Shoal as at Laysan (4.0 colonies/m^2 and 2.1 colonies/m^2, respectively). Densities of *Montipora*, faviids, and fungiids were four times greater at Lisianski/Neva Shoal than at Laysan, while densities of other taxa were comparable at the two banks (Fig. 4).

The distribution of colony sizes from Laysan and Lisianski/Neva Shoal were significantly different for *Porites* (Kolmogorov-Smirnov two-sample test, $p < 0.01$), *Montipora* ($p < 0.01$), and *Pocillopora* ($p < 0.05$). Both *Porites* and *Montipora* had a greater proportion of large colonies (> 40 cm) at Lisianski/Neva Shoal than at Laysan (31% vs. 18% for *Porites*, and 22% vs. 15% for *Montipora*) (Fig. 5). The proportion of *Pocillopora* colonies in small size classes (< 10 cm) was substantially greater at Lisianski/Neva Shoal (68%) than at Laysan (41%).

DISCUSSION

Synopsis of Salient Results

The three survey methods used in the present study produced several highly congruent findings with regards to coral community structure at Laysan and Lisianski/Neva Shoal, which in turn point to salient differences between the two banks at comparable depths and exposures to wave stress. Coral cover at Laysan was low (mean ≤ 8.2%, all three methods), with all methods yielding the highest mean coral cover along the northwestern exposure, and the lowest mean coral cover along eastern exposures. Coral cover at Lisianski/Neva Shoal was higher (mean ≥ 19.7%, all three methods), with the difference between the two banks being statistically significant for each of the three methods. The highest mean coral cover at Lisianski/Neva Shoal as determined from towed-diver surveys was along the southwest exposure (27.3%); comparable values were determined from videotransects and photoquadrats along the southwest sector (24.4% and 25.5%, respectively), but these site-specific methods yielded highest mean coral cover values on the northeast sector (38.5% and 42.7%, respectively). Because towed-diver

surveys include soft-bottom (e.g., sand) areas while site-specific surveys target hardbottom substrate, and because towed divers survey substantially more area than freeswimming divers during site-specific surveys, values derived from towed divers likely provide a better measure of mean coral cover across large expanses of habitat than do site-specific surveys.

All three methods showed statistically significant differences in the relative abundance of coral taxa among sectors at each bank and between Laysan and Lisianski/Neva Shoal. *Pocillopora* contributed little to coral cover at Lisianski/Neva Shoal but contributed a moderate amount (13.1-23.6%) at Laysan, where all methods showed its highest relative abundance on the northeast sector. Conversely, *Montipora* contributed little to coral cover at Laysan but contributed moderately (21.2-26.5%) at Lisianski/Neva Shoal, where all methods showed its highest relative abundance along eastern exposures. All methods showed that *Porites compressa* contributed less to coral cover at Laysan than at Lisianski/Neva Shoal, where it was most prevalent on the southwest exposure. Massive and encrusting *Porites* (e.g., *P. lobata*, *P. evermanni*) is the chief component of coral cover at both banks, although its relative contribution is greater at Laysan than at Lisianski/Neva Shoal (70.0-79.9% vs. 52.3-62.3%, respectively).

Two additional parameters of coral community structure, density and size class frequencies, were derived exclusively from site-specific surveys and displayed notable differences between the two banks. Overall coral colony density was twice as great at Lisianski/Neva Shoal than at Laysan, chiefly based on the effect of *Montipora*, faviids, and fungiids being four times as dense at Lisianski/Neva Shoal. Statistically significant differences between banks in the size class distribution of each of the three primary genera—*Porites*, *Montipora*, and *Pocillopora*—highlight a trend towards larger colonies of *Porites* and *Montipora* and smaller colonies of *Pocillopora* at Lisianski/Neva Shoal compared to Laysan.

Comparison with Previous Surveys

From southwest reefs, Grigg (1983) reported 18 scleractinian species from Laysan and 17 from Lisianski/Neva Shoal. Maragos et al. (2004) reported 29 scleractinian species from Laysan and 26 from Lisianski/Neva Shoal but provided no demographic data pertaining to their distribution across the banks. In the present study, six species were distinguished in videotransects or photoquadrats at Laysan and 11 were distinguished in comparable imagery from Lisianski/Neva Shoal. The dominance of *Porites lobata* at both Laysan and Lisianski/Neva Shoal in the present study is consistent with its top ranking based on the use of occurrence and abundance indices developed by Maragos et al. (2004) and with its top ranking by Grigg (1983) (Table 4). The only taxa quantified from digital imagery in the present study that are not among the top eight taxa as ranked through Maragos et al. (2004) or Grigg (1983) are *Montipora patula* and *Fungia scutaria*, at Lisianski/Neva Shoal (Table 4). Conversely, *Pavona duerdeni*, *Montipora flabellata,* and *Porites brighami* were not seen in digital imagery in the present study from Lisianski/Neva Shoal (though they were recorded outside the area captured by digital imagery), and *Pocillopora ligulata*, *Pavona duerdeni*, and *Porites brighami* were not seen

in digital imagery from Laysan (though they were also seen outside the image capture area). These discontinuities are in contrast to similar comparisons at French Frigate Shoals (Kenyon et al., 2006b) and Pearl and Hermes Atoll (Kenyon et al. in press) in which ranking results from Maragos et al. (2004), Grigg (1983), and surveys similar to those described in the present study were more congruent. This suggests that these six species are patchy in their occurrence at Lisianski/Neva Shoal or Laysan, and that observing them is more prone to bias from site selection than is observing the other seven species in Table 4 (*Porites lobata, Pocillopora meandrina, Cyphastrea ocellina, Porites evermanni, Montipora capitata, Porites compressa, Pocillopora damicornis*). Of these seven species, considerable variation exists among the three studies in their relative position within the ranking.

Table 4. Relative abundance of coral species at Laysan and Lisianski/Neva Shoal ranked by photoquadrats in this study, in Maragos et al. (2004), and in Grigg (1983).

Rank	Present Study	Maragos et al. (2004)	Grigg (1983)
		LAYSAN	
1	*Porites lobata*	*Porites lobata*	*Porites lobata*
2	*Pocillopora meandrina*	*Pocillopora meandrina*	*Porites compressa*
3	*Montipora patula*	*Montipora capitata*	*Pocillopora meandrina*
4	*Cyphastrea ocellina*	*Pocillopora ligulata*	*Montipora verrucosa*[b]
5	*Porites evermanni*[a]	*Porites evermanni*[a]	*Montipora patula*
6	N.A.[c]	*Cyphastrea ocellina*	*Cyphastrea ocellina*
7	N.A.[c]	*Porites compressa*	*Porites brighami*
8	N.A.[c]	*Pavona duerdeni*	*Pavona duerdeni*
		LISIANSKI	
1	*Porites lobata*	*Porites lobata*	*Porites lobata*
2	*Porites evermanni*[a]	*Porites compressa*	*Porites compressa*
3	*Montipora capitata*	*Porites evermanni*[a]	*Porites brighami*
4	*Porites compressa*	*Pocillopora damicornis*	*Cyphastrea ocellina*
5	*Montipora patula*	*Cyphastrea ocellina*	N.A.[d]
6	*Pocillopora damicornis*	*Montipora capitata*	N.A.[d]
7	*Cyphastrea ocellina*	*Pavona duerdeni*	N.A.[d]
8	*Fungia scutaria*	*Montipora flabellata*	N.A.[d]

[a] Considered to be *Porites lutea* by Fenner (2005).

[b] Revised as *Montipora capitata* (Maragos, 1995).

[c] Not available; only 5 species were seen in Laysan photoquadrats.

[d] Not available; data only provided for 4 species by Grigg (1983).

Grigg (1983) reported a mean coral cover of 40% from three 50-m transects off the southwest sector of Laysan. This value is very high relative to the average coral cover (6.0%) obtained from analysis of 6.6 km surveyed by towed divers along the southwest portion of the bank (Table 1, Figs. 2, 3) as well as average coral cover derived from videotransects (11.3%) and photoquadrats (11.8%) on the southwest sector (Table 2, Figs. 2, 3); the highest coral cover at any of the nine sites surveyed at Laysan was 21.2%, on the northwest sector. From two 50-m transects off the southwest sector of Lisianski/Neva Shoal, Grigg (1983) reported a mean coral cover of 24%. This value is comparable to estimates derived from analysis of 10.7 km surveyed by towed divers (27.3%) along the southwest portion of Neva Shoal (Table 1, Figs. 6, 7) and to average coral cover obtained from videotransects (24.4%) and photoquadrats (25.5%) on the southwest sector (Table 3, Figs. 6,7). Though Grigg (1983) also generalized a progressive decrease in coral cover moving northward in the NWHI, coral cover data derived from each of three independent methods in this study indicate coral cover at Lisianski/Neva Shoal is several times higher than at Laysan (Tables 1, 2, 3). These comparisons highlight the need for broad survey coverage in characterizing habitats.

Coral Cover, Relative Abundance, and Wave Stress

Coral community structure in the main Hawaiian Islands has been shown to respond to storm wave stresses of varying frequency and intensity as predicted by the 'intermediate disturbance hypothesis' (Dollar 1982). Moderate cover is attained as the result of a continual cycle of intermediate intensity disturbances, such as waves produced by storm-generated swells from the North Pacific, while high coral cover is found in sheltered embayments and areas protected from direct swells. In the NWHI, most large (5-10+ m) wave events approach the islands and atolls from the west, northwest, north, and northeast, with the highest energy waves generally occurring from the northwest sector (Friedlander et al., 2005). High-energy wave events occur primarily in the winter (November-March), with extreme wave events (10 + m waves) subjecting shallow-water coral reef communities to wave energies at least one order of magnitude greater than from the typical winter waves. More benign wave regimes in the summer are primarily driven by northeast trade winds, with wave stress greatest along northeast and eastern exposures. The southern sides of most of the islands/atolls are exposed to fewer and weaker wave events. Despite their low altitude (~ 13 m, Ely and Clapp, 1973) and relatively small sizes (each < 4 km^2, NOAA, 2003), both Laysan and Lisianski Islands provide lee to southerly reefs from both northeast trade wind-generated and northwest swell-generated seas. Grigg (1983) suggested that southwestern reefs throughout the Hawaiian Archipelago would have the highest coral cover because they experienced the greatest shelter from wave stress, but in the present study at Laysan, highest coral cover was found along the northwest sector. Coral cover was primarily composed of massive and encrusting *Porites* (> 80 %, chiefly *P. lobata,* all three methods) which, with its solid, low-relief growth form is well adapted to withstand the energy of powerful winter waves (Storlazzi et al., 2005). A similar pattern exists at French Frigate Shoals (Fig. 1), where the highest coral cover value along the perimeter of the forereef (25.8%) was found on the northwest sector, of

which the primary component (89.9%) was massive and encrusting *Porites* (Kenyon et al., 2006b). At both Laysan and along the French Frigate Shoals forereef, highest cover of *Pocillopora* (chiefly *P. meandrina*) was found along the northeast exposure. The densely-packed branches and tendency of this species to rapidly colonize newly cleared surfaces (Dollar, 1982) also suit it to surviving in the high-energy wave environments produced by prevailing northeast trade winds (Storlazzi et al., 2005). At Lisianski/Neva Shoal, the highest coral cover value determined from towed-diver surveys (which, as discussed above, is considered a better estimate of coral cover over long distances than site-specific surveys) was along the southwest sector, as suggested by Grigg (1983). The lowest coral cover value at Lisianski/Neva Shoal, determined with all three methods, was along the northwest sector. *Porites compressa*, which in the main Hawaiian Islands forms monospecific stands in embayments and other reef areas protected from wave stress (Dollar, 1982), was most prolific on the more sheltered, southern exposures of Neva Shoal. *Montipora*, whose growth form can vary considerably depending on wave stress, occurred either as encrusting or thick, plating colonies along the eastern exposure at Lisianski/Neva Shoal, well suited to wave regimes engendered by the northeast trades (Storlazzi et al., 2005).

Modern Trends in Coral Community Structure at Laysan and Lisianski/Neva Shoal

Jokiel and Rodgers (2007) used five, equally weighted metrics of coral-reef biological "health" or "value" (reef-fish biomass, reef-fish endemism, coral cover, endangered monk seal [*Monachus schauinslandi*] population, and numbers of female green sea turtles [*Chelonia mydas*] nesting annually) to rank the condition of 18 islands/atolls throughout the Hawaiian Archipelago. Lisianski/Neva Shoal ranked second to French Frigate Shoals (Fig. 1) in this integrated index of reef condition, and Laysan ranked fourth. Much of Lisianski/Neva Shoal's composite score derived from its high scores in the reef-fish endemism and coral cover categories, while much of Laysan's composite score derived from its high score in monk seal population numbers. These indices suggest the intact nature of ecological systems at these banks relative to the less healthy reefs close to human population within the main Hawaiian Islands, yet coral communities at both banks remain potentially vulnerable to stressors that may arise from distant sources, including marine debris accumulation, coral bleaching, and other disease states.

Derelict fishing gear is a chronic form of pollution affecting coral reefs in the NWHI (Donohue et al., 2001). A convergence zone associated with the North Pacific Ocean subtropical high is thought to be the mechanism by which marine debris originating throughout the North Pacific aggregates in the region of the NWHI (Kubota, 1994). In comparing rates of debris accumulation along northeastern exposures where Hawaiian monk seals tended to congregate and were thus susceptible to net entanglement, Boland and Donohue (2003) showed that debris is more readily deposited on beaches at Lisianski and Laysan compared to atolls farther north (e.g., Pearl and Hermes, Kure, Fig. 1), where debris driven over the northeast barrier reef by prevailing trade winds becomes stranded in shallow lagoon waters. Nonetheless, in passing through shallow (<

10 m) coral reef habitats before being driven ashore, debris may snag on a succession of coral heads, abrading tissue and detaching colony fragments or entire coral heads (Donohue et al., 2001). Surveys of debris occurrence and abundance on Neva Shoal at Lisianski have shown the area to be relatively debris-free compared to a model predicting its accumulation rate in comparable 'net habitat' (likely areas of accumulation based on depth, benthic habitat type, and energy regime) at atolls in the NWHI (Dameron et al., 2007). Even so, the area of predicted 'net habitat' at Lisianski/Neva Shoal (9.51 km^2) is low compared to those atolls. Marine surveys for derelict fishing gear have not been conducted at Laysan, but the predicted 'net habitat' (0.76 km^2) is minimal compared to other locations in the NWHI for which calculations have been made (Dameron et al., 2007).

Coral communities throughout the NWHI experienced bleaching in 2002 and 2004 (Kenyon et al., 2006a, Kenyon and Brainard 2006), with the highest levels of bleaching in both years at Pearl and Hermes Atoll (Kenyon et al., in press). In both years, bleaching was more severe at Lisianski/Neva Shoal than at Laysan. In 2002, surveys conducted by towed divers over deeper (> 11.6 m) offshore habitat around Lisianski/Neva Shoal revealed 22.8% of coral cover evidenced some degree of bleaching, but only 13.3% of coral cover in comparable depths at Laysan was bleached (Kenyon et al., 2006a). Shallower habitats at Lisianski/Neva Shoal (≤ 6.3m) showed higher levels of bleaching (39.5% of coral cover). *Montipora* showed differential susceptibility to bleaching at Lisianski/Neva Shoal, where 27.0% of *Montipora* cover in deeper water and 24.8% of *Montipora* cover in shallow water evidenced bleaching. At Laysan, *Pocillopora* evidenced the highest differential susceptibility to bleaching, with 39.2% of *Pocillopora* cover bleached. As elsewhere in the NWHI, massive and encrusting *Porites* were highly resistant to bleaching at both locations. Free-swimming divers conducting site-specific surveys in 2002 reported bleaching at 13 of the 15 sites examined at Lisianski/Neva Shoal, with *Montipora* again showing the greatest susceptibility to bleaching (37.9% of *Montipora* colonies). Bleaching was not seen that year, however, at any of the seven sites examined at Laysan by free-swimming divers. In 2004, bleaching incidence determined at fixed sites by free-swimming divers documented even higher levels of bleaching at both Lisianski/Neva Shoal and Laysan (Kenyon and Brainard, 2006). Taxonomic patterns of bleaching varied in 2004 from those observed in 2002, however. At Lisianski/Neva Shoal, *Porites evermanni* rivaled *Montipora patula* in the proportion of colonies affected (52.6% and 56.3%, respectively) and at Laysan, *M. patula* was the taxon most severely affected (35.5% of colonies). Both bleaching episodes were at least in part thermally induced, as they coincided with periods of prolonged, elevated sea-surface temperatures detected by satellite remote sensing and in situ temperature recorders (Hoeke et al. 2006a,b; Kenyon and Brainard, 2006). The variable nature of the taxa primarily affected at these two banks during the two bleaching episodes suggests that, should the frequency and severity of thermally induced bleaching increase in response to a warming trend in the Hawaiian Archipelago (Jokiel and Brown, 2004; Barton and Casey, 2005), all the primary hermatypic corals at these two banks are potentially susceptible to bleaching and its possible ecological consequences.

Thermal stress can increase the susceptibility of corals to coral disease and lead to outbreaks where corals are abundant (Harvell et al.,1999; Kuta and Richardson, 2002; Rosenberg and Ben-Haim, 2002; Bruno et al., 2007). Of four disease syndromes affecting *Porites* and three affecting *Montipora* throughout the NWHI, two of the *Porites* syndromes and one *Montipora* syndrome have been documented at Laysan, with the same two *Porites* syndromes documented at Lisianski/Neva Shoal (Aeby, 2006). Average disease prevalence (proportion of colonies affected) is low throughout the NWHI (0.5%), with the lowest prevalence at Lisianski/Neva Shoal (0.2%) and more than twice as high prevalence at Laysan. However, both banks show the highest frequency of occurrence of coral disease (proportion of sites affected), with disease present at all sites examined at both locations (Aeby, 2006). Disease levels in the NWHI are much lower than those reported for other reefs in the Indo-Pacific (e.g., Willis et al., 2004) and the Caribbean (Weil, 2004) and may represent normal levels of disease expected on a healthy reef with minimal impacts from anthropogenic stress. However, disease levels are increasing on other reefs throughout the Indo-Pacific, and the emergence of new marine diseases raises questions as to how they are being transported among reefs (Aeby, 2007).

Although these data represent the most spatially extensive and detailed surveys to date, it is recognized that every scientist works within the suite of possibilities and constraints afforded by the research questions, technology, and financial resources of the times. These surveys, and the results thereby generated, build on several previous investigations of the distribution and community structure of corals in the NWHI (Vaughan, 1907; Grigg, 1983; Maragos et al., 2004). In their time, they stand as the most complete and detailed description of coral community structure at Laysan and Lisianski/Neva Shoal. It remains for future scholars of coral reef ecology, acting with the technologies, resources, opportunities, and limitations of their time, to build on these results and further weave them into the fabric of science.

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